# REPRODUCTIVE BIOLOGY IN DULOTIC ANTS: PRELIMINARY REPORT (HYMENOPTERA: FORMICIDAE)[1]

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Ant workers are ordinarily sterile females with reduced ovarioles. They may be able to lay eggs in the presence of the queen, but the eggs laid by these workers are specialized trophic eggs which usually serve no purpose other than to provide protein for the queen and larvae. However, in queenless colonies workers are known to lay eggs which in most cases develop into males. This inhibition of worker ovarian development has been observed thus far in *Leptothorax* (Bier, 1954), *Formica* (Bier, 1956), *Plagiolepis* (Passera, 1965), and *Myrmica* (Mamsch and Bier, 1966). The phenomenon of queen control is also found in other social insects. At least two inhibitory pheromones (both produced in the queen's mandibular glands) are involved in queen control in honeybees (Butler, 1957). One of these pheromones has been identified as 9-oxodec-*trans*-2-enoic acid (Butler et al., 1961). No queen control pheromone in ants has yet been identified.

The practice of slavery or dulosis in ants is unique among insects. Ants of the genera *Harpagoxenus, Strogylognathus, Myrmoxenus (?), Leptothorax, Formica, Polyergus,* and *Rossomyrex* are known to raid colonies of other species for their worker brood and use them as slaves after they emerge into adults (Wilson,

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1971). Two types of dulosis are known (Wheeler, 1910). In the faculative slave-makers the colonies are sometimes found without slaves. In the obligatory slave-makers, however, the ants are wholly dependent on their slaves so that they are even incapable of obtaining their own food. The ovarian development of both master workers and slaves is of course restricted by the queen(s) of the slave-maker species. Here I present two cases in which the production of lsave progeny is inhibited by the presence of their master workers in queenless colonies.

Workers of the facultative slave-maker, *Formica pergandei* (acc. no. 71-11) with their slaves, *Formica canadensis,* were collected at Oakville Prairie, the University of North Dakota biological field station located 12 miles west of Grand Forks, on 14 September 1971 and maintained in the laboratory for 3 months. It was hoped that any effects the queen or queens of the original colony may have had on these workers (both masters and slaves) would have disappeared during this 3 month separation from the original colony. On 19 December 1971 this colony fragment was divided into 3 parts and kept in 1-gallon jars with soil preheated to avoid contamination of brood from the original nest. Both master and slave workers were used in nests 71-11A and 71-11B, but only slaves in nest 71-11C. These 3 nests were then kept in a refrigerator at 4°C for two weeks. After this treatment they were moved into the laboratory, kept at room temperature (= 20 – 25°C), and fed with an artificial diet consisting of a mixture of whole, raw egg and honey.

Males emerged from both 71-11A and 71-11B on 15 March 1972 and from 71-11C on 30 March 1972. When this experiment was concluded on 5 May, a total of 23 males were collected from nest 71-11A, 31 from nest 71-11B, and 7 from nest 71-11C. There were 27 master workers and 104 slaves remaining in 71-11A and 33 slaves in 71-11C at the conclusion of the experiment (no initial number of ants in each nest was recorded). No brood was present in any of these two nests. Nest 71-11B was not opened at this time. It was kept in a refrigerator at 4°C for 10 days and then moved back into the laboratory in hopes that the workers would lay eggs again. One male was collected from this nest on 27 May 1972. This male was probably left over from the first brood. When

this nest was opened on 13 August 1972 there were 27 master workers and 168 slaves and no brood.

The males collected from both 71-11A and 71-11B (i.e., the nests with both master workers and slaves) are all *pergandei* (those from 71-11C are of course all *canadensis).* This seems to indicate that in the presence of the master workers no adult males of the slave species are produced.

To test this hypothesis workers of the obligatory slave-maker, *Polyergus breviceps* (acc. no. 72-1), and their slaves, *canadensis,* were collected from Oakville Prairie on 19 May 1972 for a similar experiment. This colony fragment was divided into 7 parts. 35 *breviceps* workers and 35 slaves were used in each of the first 5 nests (72-1-A to E) and only 70 slaves each were in the last 2 (72-1-F, G) to serve as control. The first male emerged from nest 72-1F on 16 July 1972. When this experiment was concluded on 21 August 1972, the following males were collected: 4 from A, 9 from B, 6 from C, 6 from D, 6 from E, 3 from F, and 2 from G. Again, only males of *breviceps* were collected from nests A through E where both master and slave workers were used.

It thus appears that after the removal of the slave-maker queen the master workers take over the control and in turn inhibit the production of slave adults in the queenless colony. This is not the same as in the case of reproductive inhibition of parasitic queens over their hosts found in some parasitic ants such as *Plagiolepis xene* (Passera, 1969). The only comparable case was found in the slave-maker *Harpagoxenus americanus,* in which one of the master workers assumes the reproductive functions in the secondary colony after losing contact with the home nest (Wesson, 1939). However, the production of unusually high number of female brood by these presumably virgin workers and the fact that *americanus* will mate in the nest seem to suggest that these reproductive workers might have already been inseminated as in the case of the European species, *H. sublaevis* (Buschinger, 1968) before establishing the secondary colony, in spite of Wesson's claim to the contrary. If this is true, then these impregnated workers will certainly assume a dominant status over the slaves in the absence of the queen(s). Since I found no female brood in the two cases studied, I assume that no inseminated workers were involved.

Further investigations on the nature of this inhibition are now in progress. These include an observation nest #71-11 D-1 established on 26 October 1972 using *pergandei* workers with *canadensis* again as their slaves. Although this nest is still under observation, some established facts regarding the behavior of both slaves and master workers can be pointed out in this preliminary report.

As of 3 January 1973 I spent a total of 40 hours and 45 minutes observing ants in this nest through green glass. During this period I saw *pergandei* workers laying both normal and trophic eggs 43 times, but I have only two rather dubious records for their slaves. Among those eggs laid by *pergandei,* 11 were eaten by *pergandei* themselves, 2 by both *pergandei* and slaves (Figs. 1-4), and 2 were given directly to the larvae. As shown in Fig. 3, some slaves also have gasters as extended as those of egg-laying *pergandei.* Dissection of these slaves has shown that they also have well developed oocytes.

On 18 December 1972 one *pergandei* was seen carrying an egg on the glass wall of the observation nest. Later she bent over and touched her anus with that egg, dropped the egg to the floor, pulled an egg out of her anus, and then walked away with the new egg. Several *pergandei* tried to take that egg away from her without success. Finally, she reached the brood pile and fed that egg to a larva for about 2 minutes and then finished up on it herself. Another *pergandei* came over and solicited food from her, but she did not give her any. This first *pergandei* again bent over and licked her anus. Then, one rather elongated egg came out. She did not pick up this egg, but just left it on the glass wall beneath her (Fig. 5). Six mins later she picked up the egg and stood there while other ants were feeding the larva nearby. She then walked toward the larva and put that egg on the glass wall near the larva and left (Fig. 6). Another *pergandei* came over carrying an egg which she fed to the larva. At this time the *pergandei* worker's head was almost touching the elongated egg laid by the first *pergandei* (Fig. 7). Thus, it appears that the elongated egg was a normal egg which the first *pergandei* laid soon after she had laid a trophic egg. A total of 7 cases were observed in which one ant laid more than one egg in a short period. In some cases the second egg came out so

soon that the ant had to receive it when the first egg was still between her mandibles (Fig. 8).

My observations also revealed several behavioral patterns of *pergandei* toward their slaves. Although *pergandei* will drag each other around, it is more often that *pergandei* will drag the slaves either by their antennae or legs (Fig. 9). Also there were 52 cases in which slaves were carried by *pergandei* (Fig. 10) in the typical formicine fashion (Wilson, 1971). Yet no *pergandei* has been seen carried in this manner by either other *pergandei* or by slaves. This might indicate a subordinate status in slaves.

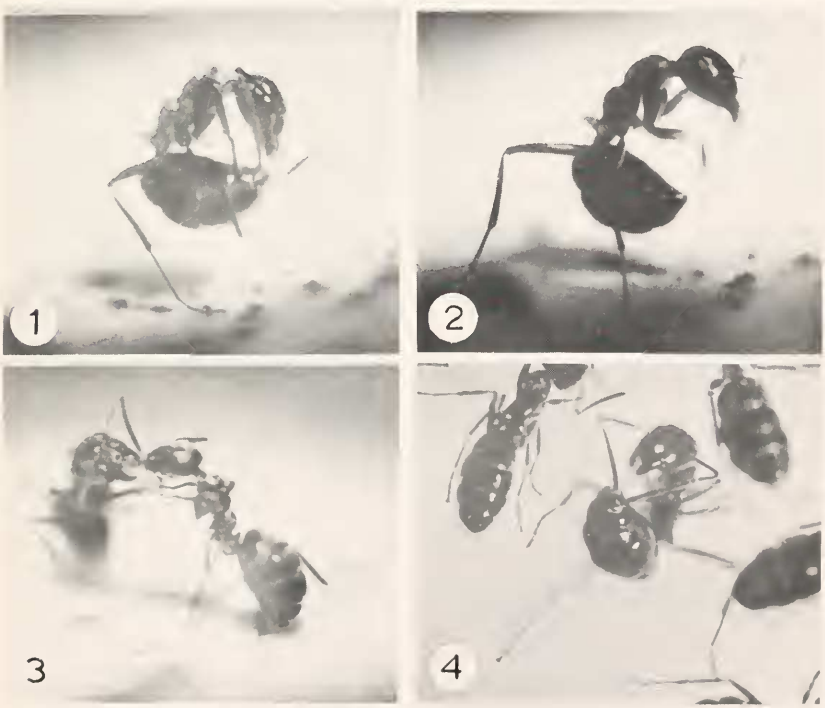
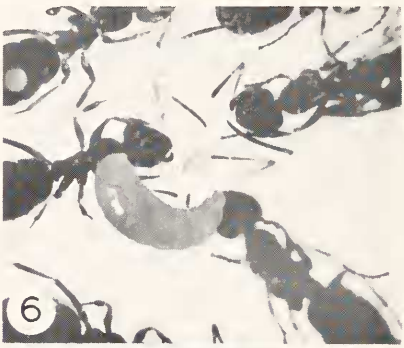
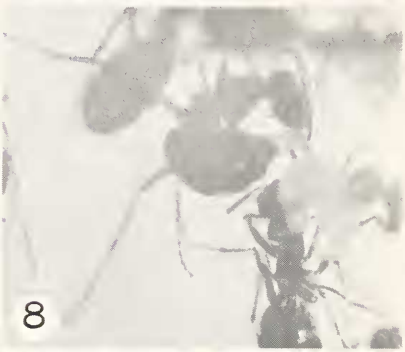



Fig. 1. Worker of *pergandei* beginning to lay egg. Note the wide-open anus.
Fig. 2. The same worker carrying the egg she has just laid.
Fig. 3. Same worker sharing that egg with a slave. Note the extended gaster of the slave.
Fig. 4. Another *pergandei* worker with a trophic egg just pulled out from her anus.







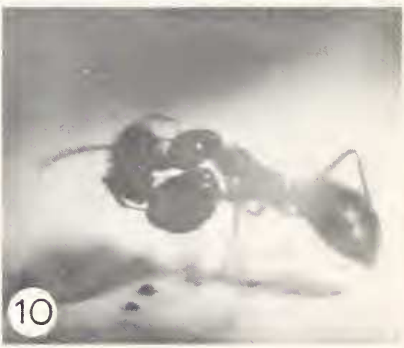



Fig. 5. One *pergandei* worker and a normal egg just laid on the glass wall beneath her.
Fig. 6. The same worker after placing that egg near a larva.
Fig. 7. Another *pergandei* worker feeding the same larva. Note the proximity of the worker's head to the normal egg.
Fig. 8. One *pergandei* worker receiving her second egg although the first egg is still between her mandibles.
Fig. 9. *Pergandei* worker dragging a slave by her hind leg.
Fig. 10. *Pergandei* worker carrying a slave in the typical formicine fashion.

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**ABSTRACT.**—Reproductive biology in dulotic ants: Preliminary report (Hymenoptera: Formicidae). Queens of the slave-maker ants, *Formica pergandei* and *Polyergus breviceps,* restrict the ovarian development of their workers and slaves. When queens are removed, the workers of the slave-maker species in turn inhibit the production of slave progeny.

Workers of *Formica pergandei* lay both normal and trophic eggs in queenless colonies. A normal egg can be laid immediately after a trophic egg. Trophic eggs are either eaten by *pergandei* workers themselves, or fed to the larvae and slaves. Only slaves are carried by *pergandei* in the typical formicine fashion.—A. Chang-Fu Hung, Department of Biology, University of North Dakota, Grand Forks, N. D. 58201.

*Descriptors:* Hymenoptera; Formicidae; *Formica pergandei; Formica canadensis; Polyergus breviceps;* dulosis; reproductive inhibition; trophic egg; behavior.